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THE FERN GAZETTE

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Volume 20 Part 4

2016

THE FERN GAZETTE is a journal of the British Pteridological Society publishing peer-reviewed papers on all aspects of pteridology.

Manuscripts may be submitted, and books etc. sent for review, to: Prof. M. Gibby, Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, EH3 5LR, UK. FernGazette@eBPS.org.uk

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THE FERN GAZETTE Volume 20 Part 3 was published on 11th July 2016

Published by THE BRITISH PTERIDOLOGICAL SOCIETY

c/o Department of Life Sciences,

The Natural History Museum, Cromwell Road, London SW7 5BD, UK

Printed by Bishops Printers Ltd

Walton Road, Portsmouth, Hampshire PO6 1TR

<http://www.bishops.co.uk>

Mailed by The Mailing People

Unit 10 Eastern Point, Fitzherbert Road, Farlington, Portsmouth, Hampshire, PO6 1RU

<http://themailingpeople.co.uk>

Cover design by Hazel Stiles

**DECAPLOID GAMETOPHYTE FORMATION FROM SPORES OF A
PENTAPLOID *CYSTOPTERIS FRAGILIS* (CYSTOPTERIDACEAE)
COLLECTED IN MONGOLIAN ALTAI**

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Key words: *Cystopteris fragilis*, decaploid, meiosis, pentaploid, sporogenesis

ABSTRACT

Germinating spores were obtained from a pentaploid *Cystopteris fragilis* collected in Mongolian Altai. DNA content of nuclei in gametophytes showed for the first time that gametophytes that developed from spores of the pentaploid sporophyte had a larger number of genomes than those of the mother sporophyte, and some appeared to be decaploid. Fertile decaploid ($10n$) spores may be produced in the pentaploid *C. fragilis* and derived from monad spores observed in sporogenesis. Antheridia were produced on the $10n$ gametophytes, although antherozoids with swimming ability were not observed. Archegonia were not observed. Apogamous sporophytes with $10n$ genome content were induced from decaploid gametophytes. The monad spores produced may contribute to the formation of higher polyploid sporophyte series in ferns.

INTRODUCTION

Cystopteris fragilis (L.) Benth. collected in Mongolian Altai showed three cytotypes, tetraploid, pentaploid and hexaploid, and although numerous univalent and bivalent chromosomes were observed in the spore mother cells of the pentaploid *C. fragilis* ($2n = 5x = \text{ca. } 210$), some germinating spores were obtained from the sporophyte (Kawakami *et al.*, 2010). In the present paper, therefore, we aimed to investigate the genome contents of germinating spores produced and also to determine how these viable spores are produced in the pentaploid sporophyte. From the results of DNA contents of nuclei in gametophytes raised from spores of the pentaploid sporophyte, it was shown for the first time that the gametophytes produced had not the same but a larger number of genomes than those of the mother sporophyte, and surprisingly, some gametophytes had decaploid

(10n) genome contents. The results might indicate that 10n spores are produced in the sporophyte and that they derive from monad spores observed in sporogenesis. In the present study, not only decaploid spore formation but also other viable spore formation processes are discussed. Furthermore, since polyploidy is one of the outstanding features in ferns (Manton, 1950; Lovis, 1977; Walker, 1979; Takamiya, 1996; Kato, 1997), we also investigated the gametophytes cultivated on agar to determine whether or not these spores could contribute to the formation of higher polyploid sporophyte series in *C. fragilis*.

MATERIALS AND METHODS

Cystopteris fragilis was collected in Mongolia, west of Hovd Province, Erdeneburen sum, N 48° 38'69", E 091° 07'74", alt. 2450 m (Kawakami *et al.*, 2010), and then cultivated in Japan. Spores collected were used for axenic culture. Gametophytes were cultivated on 1/4 strength of Murashige and Skoog (1962) (MS) medium supplemented with 0.75 % sucrose and 0.7 % agar. For the apogamous sporophyte formation, gametophytes were transplanted on 1/4 strength of MS medium supplemented with 3 %

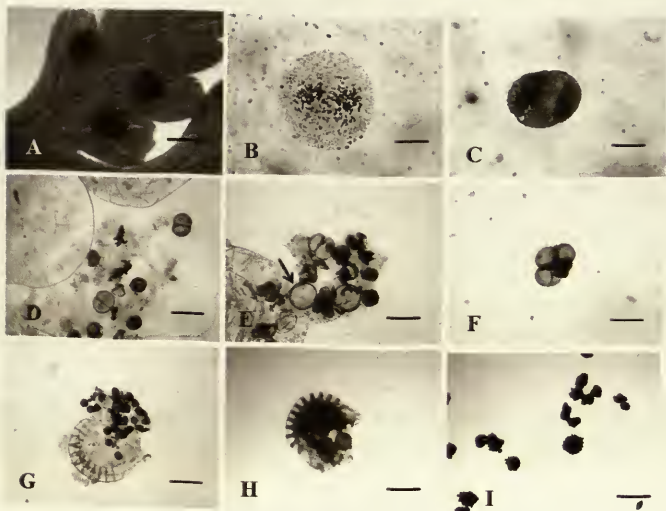


Figure 1. Sporogenesis in pentaploid *Cystopteris fragilis*, A: sporangia on the underside of the frond; B: meiotic chromosome separation; C: two nuclei formed by chromosome separation; D: dyad spores produced in a sporangium; E: young spores produced in a sporangium, arrow indicates a monad spore; F: four spores in a tetrad; G: sterile spores produced in one sporangium; H: a large round spore with spiked ornamentation produced in a sporangium; I: spores collected from the pentaploid sporophyte, arrow indicates a fertile spore. Scale bars: A: 1 mm; B, C: 10 μ m; D, E: 50 μ m; F: 25 μ m; G, H, I: 100 μ m.

sucrose, 0.1 % casamino acid and 0.8 % agar. Cultures were maintained at 25 °C and illuminated by two fluorescent lamps (NEC FL 15BR) to keep 800 lux at the surface. Meiotic chromosomes were observed by fixing sporangia with 3:1 ethanol-acetic acid for 30 min at 5 °C and squashing them in 2 % aceto-orcein solution. The DNA contents of nuclei in fronds were estimated by flow cytometry using a Partec Ploidy Analyzer PA (Partec, Münster, Germany) (Kawakami *et al.*, 2003).

RESULTS

The pentaploid *Cystopteris fragilis* produced sporangia on the underside of the frond (Figure 1A). In spore mother cells, numerous univalent and bivalent chromosomes were observed at meiotic metaphase I. By meiotic chromosome separation (Figure 1B) two nuclei were formed (Figure 1C), and dyad spores were observed frequently in sporangia (Figure 1D). Some of these consisted of both large and small spores. Monad spores (Figure 1E) and spores in tetrads (Figure 1F) were more rarely observed. Mostly, young spores produced in sporangia did not mature and the sporangia did not develop (Figure 1G). In a few expanded sporangia, a few large spores with spiked ornamentation were observed (Figure 1H). Although spores obtained were mostly abortive, some were able to germinate (Figure 1I).

DNA contents of nuclei in 13 gametophytes derived from spores of the pentaploid sporophyte were investigated. Their genome contents were greater than those of the donor pentaploid sporophyte (Figure 2A). Two gametophytes had approximately $8n$ genome content (Figure 2B), another two had approximately $9n$ and nine gametophytes had approximately $10n$ genomes (Figure 2C).

Eight out of nine $10n$ gametophytes produced antheridia (Figure 3A), however, swimming antherozoids were not observed. Archegonia were not observed on any gametophytes during three years of culture. Apogamous sporophytes were induced from two $10n$ gametophytes after one year of culture (Figure 3B). They grew to approximately 10 mm in height but then died.

DISCUSSION

Manton (1950) made a cytological study of the pteridophyta, and following her, similar investigations on pteridophyta were carried out by many researchers (e.g. Wagner, 1954; Lovis, 1964; Sleep, 1966, 2014^{*}; Reichstein, 1981; Pinter, 1995; Ekrt & Koutecky, 2016). In these studies, various suggestions have been proposed about differentiation and development in ferns through observations of meiosis in hybrid species.

Generally speaking, meiosis of sporophytes with many univalent chromosomes is irregular and spores produced are mostly abortive. If fertile spores could be obtained from those sporophytes, one might consider whether they are reduced spores with aneuploid chromosome numbers, as reported in triploid *Osmunda regalis* L. (Manton, 1950) or unreduced spores with the same chromosome number as the mother plant, produced by the pathway of Döpp-Manton or Braithwaite (Manton, 1950; Braithwaite, 1964; Walker, 1979; Kato, 1997; Kawakami *et al.*, 2003). In the present study, however, the genome contents of gametophytes developed from spores of the pentaploid *C. fragilis* were greater than those of the donor pentaploid sporophyte and some gametophytes had

* Sleep examined *Polystichum* and proposed her ideas on the development of this genus. Her studies were not limited to *Polystichum* but also extended to other ferns. Because of her early death, this study (Sleep, 2014) was published posthumously.

$10n$ contents that double the genome contents of the donor sporophyte. Since gametophytes develop directly from spores, their genome content must be considered to be the same as that of the spore from which an individual is derived. The results, therefore, suggest that spores with a higher ploidy level than the mother sporophyte are, surprisingly, produced in the pentaploid *C. fragilis*. The formation of gametophytes with genomes doubled that of the donor sporophyte is reported here for the first time.

From the observation of meiosis, it might be considered that spores with $10n$ genome

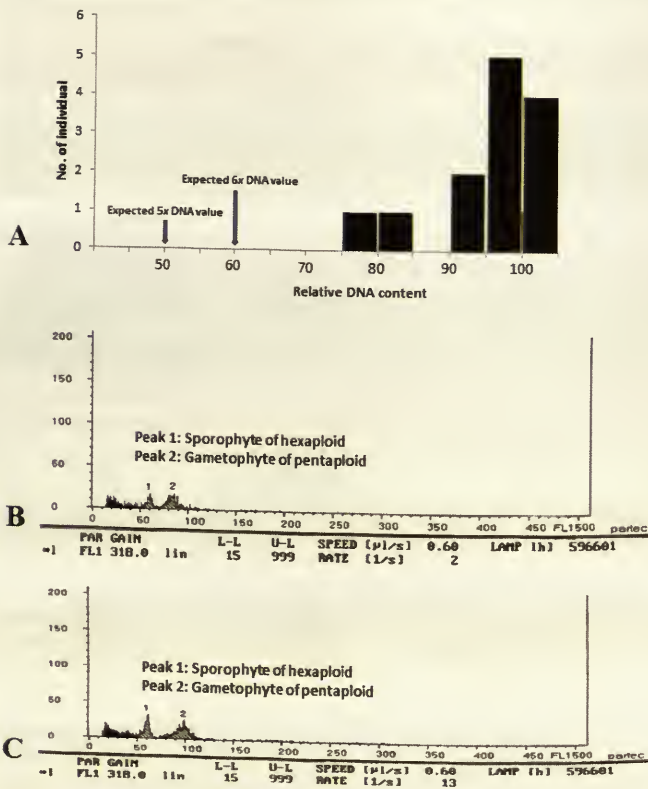


Figure 2. Relative DNA content of gametophytes derived from spores of the pentaploid *Cystopteris fragilis*, A: distribution of relative DNA content of 13 gametophytes; B: sample of gametophytes with approximately $8n$ genome contents; C: Sample of gametophytes with approximately $10n$ genome contents.

contents are from monad spores produced in sporangia. They might be produced without meiotic cell division from the spore mother cells with doubled genome contents. When monad spores are produced, restitution nuclei might occur; and if some chromosomes are lost when they occur, monad spores with genomes smaller than $10n$, for example, $9n$ or $8n$, might be produced. However, in the formation of spores with $9n$ or $8n$ genome contents, especially in the case of $8n$ spore formation, another pathway might be considered. Since in sporogenesis dyad spores consisting of large and small spores were observed in the present study, the larger spore with $8n$ might be fertile, though the smaller spore with $2n$ might be sterile. Although dyad spores are well known to be produced in many ferns, they are unreduced spores with the same genome contents as the donor sporophyte (Walker, 1979; Kato, 1997; Kawakami *et al.*, 2003). Why fertile $5n$ spores were not obtained in this study is unknown. Further studies of fertile spores may be required to understand sporogenesis of the pentaploid sporophyte. The present study revealed the monad spore formation in the pentaploid *C. fragilis*.

It is well known that polyploidy is one of the outstanding cytological features in ferns (Manton, 1950; Wagner, 1954; Lovis, 1968; Walker, 1979; Kato, 1997). The highest polyploid fern in Japan is $10x$ (Nakato, 1987; Takamiya, 1996) and the highest polyploid in the world is reported to be $16x$ (Walker, 1979). The evolutionary process of how polyploid ferns such as $10x$ or $16x$ are produced has not been investigated in detail. Since unreduced spores are well known to play a very important role for polyploid formation (Gastony, 1986; Kato, 1997), the pathway of the decaploid sporophyte ($10x$) formation could well be that they are produced by fertilization of pentaploid gametes produced from pentaploid gametophytes derived from unreduced spores produced in pentaploid plants. The present study, however, may well indicate another method of decaploid sporophyte formation: the pentaploid sporophytes produce decaploid spores and from decaploid gametophytes developed from spores, decaploid sporophytes could be induced apogamously. Furthermore, if antherozoids with an ability of fertilization could be produced from the decaploid gametophytes, though these were not observed in the present study, it might be possible to produce plants with higher polyploid levels than decaploid, such as $12x$ plants, by fertilization between decaploid male gametes and female diploid gametes derived from tetraploid sporophytes. Whether the fertile spores produced in pentaploid sporophytes can play a role in the formation of higher polyploid

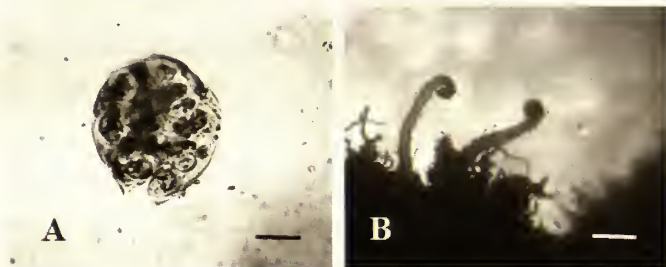


Figure 3. An antheridium with antherozoids (A) and apogamous sporophytes (B) produced on gametophytes with approximately $10n$ genome content in *Cystopteris fragilis*. Scale bars: A: 25 μ m; B: 1 mm.

C. fragilis in nature or not is quite intriguing. If decaploid *C. fragilis* were discovered in Mongolian Altai, it might have been produced from decaploid gametophytes apogamously. To understand the evolution of polyploidy in these ferns, further studies on *C. fragilis* in Mongolian Altai may be necessary. .

ACKNOWLEDGEMENT

The study was supported by a Grant-in-Aid for Scientific Research Program (A) 19255004 (the representative: Katsuhiko Kondo) from the Japan Society for the Promotion of Science.

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SHORT NOTE

TWO UPDATES FOR GRAMMITID FERNS (POLYPODIACEAE) ON THE 'FERNS OF THAILAND' WEBSITE

The Ferns of Thailand website (<http://rbg-web2.rbge.org.uk/thaifers/Pages/thai-fern-list.htm>), updated 23 June 2016, has one wrongly named set of images and one species that has been re-identified amongst the grammitid ferns (Polypodiaceae).

The on-line image of *Prosaptia celebica* is not of that species, but belongs to *Ctenopterella blechnoides*: the voucher specimen is Middleton et al. 5332 (E00700990!). The red-brown rhizome scales characteristic of most species of *Ctenopterella* can be seen in one of the images; in detail they are concolorous and glabrous. The rhizome scales of *Prosaptia celebica* are subclathrate to clathrate, medium to dark red-brown and ciliate.

Thailand material formerly identified as *Prosaptia alata* (Middleton 4400 E00700991!, Middleton E00690558!) has been re-identified as *P. serriformis*. The former has the rachis prominent and concolorous on the adaxial surface and sori in cylindrical pouches, while the latter has the rachis slightly prominent to slightly sunken and concolorous to darker on the adaxial surface and sori in hemispherical or conical pouches. Peninsular Malaysian material of *P. alata* has also been re-identified as *P. serriformis*.

ACKNOWLEDGEMENTS

I wish to thank the Curator of the herbarium, Royal Botanic Garden Edinburgh for permission to examine specimens of Grammitids in July 2016.

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TWO NEW RECORDS FOR COLOMBIA OF *PSILOTUM NUDUM* (PSILOTACEAE) FROM THE MAGDALENA VALLEY AND IN THE ANDEAN AMAZONIAN FOOTHILLS

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Key words: Inconspicuous species, Caldas, Caquetá, ferns, distribution.

ABSTRACT

Despite its wide distribution, *Psilotum nudum* has been recorded previously only from the western slopes of the Occidental Andean Cordillera of Colombia, particularly in the Chocó Region, and in the Caribbean Golf of Urabá. As a result of recent exploration, we here expand the distribution of *P. nudum* in Colombia by reporting two new records from the Central and Oriental Andean Cordilleras.

INTRODUCTION

Psilotum nudum (L.) Beauv. is a remarkable fern taxon and the simple aerial axis was widely regarded as a possible ancestral shoot design for sporophyte land plants (Figure 1) (Bierhorst, 1977; Gensel, 1977; Schulte et al., 1987). The relationships among Ophioglossales, Marattiales, Psilotales and extinct taxa (Cladoxylales, Zygopteridales, Iridopteridales, Stauropteridales) remain highly ambiguous (Gensel, 1977; Bateman et al., 1998). However, based on more recent molecular analyses, it is currently classified in the family Psilotaceae as a sister group of Ophioglossaceae, with both included in the class Psilotopsida (Smith et al., 2006). These molecular results are supported by evidence from morphology, for example, both families have cylindrical subterranean, non-green, mycorrhizal gametophytes and possess sporangia that are born on the adaxial surface of the leaf (Moran, 2004).

Psilotum nudum has a wide distribution, which is principally pantropical (Tryon & Tryon, 1982; Mickel & Smith, 2004), but it can be distributed in the subtropics of Australia and New Zealand (AVH, 2016) and in the more temperate zones of Spain (Molesworth-Allen, 1966; Galan et al., 1996). It can be found from sea level up to 1840m (Idárraga-Piedrahita et al., 2014; Murillo et al., 2016; TROPICOS, 2016). In America, it has been recorded from the south of the United States of America, Mexico, Central America, Colombia, Venezuela, Guayanas, Ecuador, Peru, Bolivia, Brazil, Paraguay, Argentina and in the Antilles (Mickel & Smith, 2004; Murillo et al., 2008; Moran 2011). It can be found either in pristine forest or urban zones (Moran, 2011).

The taxon may have few records in Colombia due to the fact that it does not look like a fern (Moran, 2004) and it prefers to inhabit places in the shade (Galan et al., 1996). Both decrease the probability of its discovery, especially for the non-trained botanist. In

Colombia, until now, it was recorded only from four localities in the Occidental Cordillera and in the Caribbean Golf of Urabá, principally in the Chocó Region (Table 1, Figure 2).

As a result of a botanic exploration in the Magdalena Medio region and in the Andean Amazonian foothills, it was discovered growing as an epiphytic fern in two new locations (Table 1, Figure 2). However, the habit of the plant can be epiphytic, terrestrial or

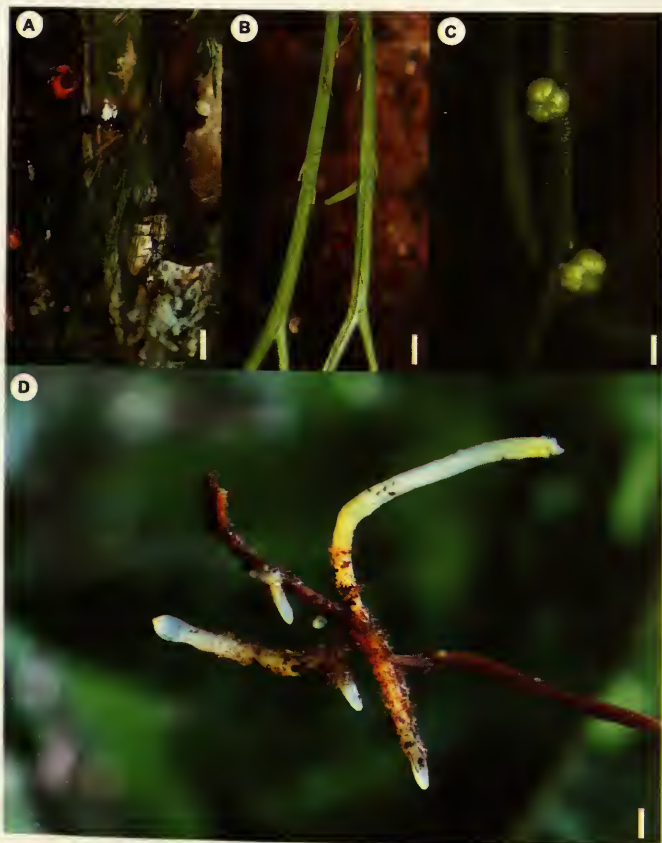


Figure 1. *Psilotum nudum*. A: Habit of the plant, scale bar (2 cm). B: Stem and leaves, scale bar (5 mm). C: Sporangia, scale bar (1 mm). D: Ramification of the rhizome, scale bar (5 mm). All from D. Sanín & J. L. Peña 6046 (COL). Photos by J. L. Peña.

lithophytic (Galan et al., 1996; Windisch, 1997). Interestingly, this taxon can be found erect or pendulous, which may depend on the environmental conditions of the locality (see TROPICOS, 2016). A most suitable place to find this species is in the axes of the leaves of palm trees (Windisch, 1997; Moran, 2004), and we have found the new records on *Bactris* sp. or *Elaeis guineensis* Jacq. (Figure 1A).

It was suggested that reports of this taxon from Antioquia, Colombia reflected the fact that it was cultivated here (Idárraga-Piedrahita et al., 2014), but these new records provide supporting evidence that it can grow wild here as proposed by Moran (2004).



Figure 2. Distribution of *Psilotum nudum* in Colombia. The black dots are previous records: 1) Apartadó, 2) Medellín, 3) Chocó, 4) Valle del Cauca and 5) Cauca. The asterisks are the new records in: the Central and Oriental Andean Cordillera of Colombia from 6) Norcasia-Caldas and 7) Florencia-Caquetá.

Table 1. Records of *Psilotum nudum* in Colombia.

Localities	Altitude (m)	Collection	Collection date	Bibliography
Antioquia: Apartadó y Medellín.	0-1500	J. Santa 378 (HUA)	Not provided	Idárraga et al. (2014).
Chocó: Nuquí-Panguí. Playa La Olímpica.	0	A. Gómez et al. 500 (MO)	14 Jan. 1992	TROPICOS (2016).
Cauca: Guapi, Orillas del río Guapi: Población de Guapi.	5	B. R. Ramírez P. 17461 (CAUP)	16 Nov. 2003	Ramírez & Macías-Pinto (2007).
Valle del Cauca: Buenaventura, Bahía de Buenaventura.	0	E. P. Killip 35510 (COL)	05 Apr. 1939	Murillo et al. (2016).
Caldas: Caldas, Norcasia, Vereda Quebra de Roque, Reserva Riomanso, desviación a mano izquierda de la Quebrada la Tostada.	224	D. Sanín, A. F. Bohórquez-O., J. Ramírez-G., V. Ramírez-V. & J. P. Betancur 5539 (HUA)	2 Dic. 2011	Current record
Caquetá: Florencia, Jardín Botánico Uniamazonia, Sendero de la Anaconda.	269	D. Sanín & J.L. Peña 6046 (COL)	14 Jul. 2015	Current record

The discovery of these populations of *Psilotum nudum* in Caldas and Caquetá department expand its distribution to the Central and Oriental Andean Cordilleras of Colombia (Figure 2), and suggest that the plant may have a wider distribution in Colombia. However, due the difficulties of recording it, its real distribution is still not well known.

ACKNOWLEDGEMENTS

DS would like to thank the University of the Amazonia for the funding support. DS is indebted to the Biology program, especially to Professor Alexander Velasquez-Valencia and the staff of the Natural History Museum of the University of the Amazonia for providing infrastructure to develop the research. The photographs were kindly provided by J.L. Peña. We thank Professor E. Trujillo Trujillo, for generously providing literature and support in the initial phases of this research. We are grateful to Professor Mary Gibby for her kind comments that improved our manuscript.

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SHORT NOTE

**TWO NEW COMBINATIONS IN GRAMMITID FERNS
(POLYPODIACEAE): *PROSAPTIA HORNEI* AND *RADIOGRAMMITIS
SETULIFERA***

Two new combinations in Asian-Pacific Grammitid ferns are proposed: *Polypodium hornei* (Baker) Parris and *Radiogrammitis setulifera* (Alderw.) Parris. A lectotype is chosen for *Polypodium hornei* Baker. Herbarium abbreviations follow Thiers (2016).

***Prosaptia hornei* (Baker) Parris, comb. nov.**, based on *Polypodium hornei* Baker, J. Bot. 17: 298 (1879). Type: Fiji, Viti Levu between Nadrau & Babuca, c. 1000 ft alt., *Horne* 369 (lectotype K! barcode 001044319, chosen here). Syn. *Ctenopteris hornei* (Baker) Brownlie, Pacific Sci. 14: 402 (1960), *Tomophyllum hornei* (Baker) Parris, Kew Bull. 65(1): 124 (2010).

Baker's description mentions two localities for the species, "Nadrau to Babuca, Viti Levu", and "mountains of Ovalau". The type sheet at Kew bears two plants; the left hand one (K001044319) is well pressed and bears a label beneath it reading "on trees Nadrau to Babuca". This plant is chosen as the lectotype. The right hand plant (K000604741) has rolled up fronds with the pinnae pressed together to obscure their abaxial surfaces and it has no label indicating its provenance.

Baker (1879) and Brownlie (1977: 359) both describe the rhizome scales of the species as ciliate, a character common to *Prosaptia* and some species of *Tomophyllum*. The type material of *Polypodium hornei* has a dorsiventral rhizome with stipes in two rows and articulated to prominent phyllopodia, and it also lacks hydathodes on the vein endings on the adaxial surface of the lamina, all of which are characters of *Prosaptia*. Brownlie's illustration of part of the frond (1977: 355, pl. XLI, 3, as *Ctenopteris hornei*) shows the crenulate pinna margin often found in *Tomophyllum*, but very rarely in *Prosaptia*, and material collected by him in CHR has the radial stipe arrangement of *Tomophyllum*. Nakamura & Kokubo (2008: 256, pl. 99, 1) illustrate (as *Ctenopteris hornei*) a plant that is obviously a species of *Tomophyllum*; it has the evident hydathodes on the vein endings on the adaxial surface of the lamina characteristic of *Tomophyllum*, the same slightly crenulate lamina margin that Brownlie illustrated, and rhizome scales with a single apical hair that are found in numerous species of *Tomophyllum*. Clearly, two species have been confused under the name *Ctenopteris hornei*; *Polypodium hornei* = *Prosaptia hornei*, and an un-named species of *Tomophyllum*. The confusion is partly due to the fact that *Prosaptia hornei* is one of a small group of *Prosaptia* species that have superficial sori (like *Tomophyllum*), as opposed to sori sunken in steep-walled depressions on the abaxial surface of the lamina or in marginal to submarginal pouches that are typical of *Prosaptia*.

***Radiogrammitis setulifera* (Alderw.) Parris, comb. nov.**, based on *Polypodium setuliferum* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16: 32 (1914). Syntypes: Malacca, *Matthew* 408 (BO); Sumatra, Barisan Mts, *Matthew* 651 [657 in K] (BO, K000501091!), Jan. 1913, *Matthew* s. n. (E00194034! p. p.). Syn. *P. pumilum* Brause, Bot. Jahrb. Syst. 49: 38 (1912) non Cockayne (1909). *Xiphopteris setulifera* (Alderw.) Parris, Kew Bull. 41(1): 69 (1986); *Oreogrammitis setulifera* (Alderw.) Parris, Gardens' Bull. 58(2): 268 (2007).

Detailed examination of the rhizomes of *Matthew* s. n in E and *Matthew* 657 in K shows that they are radial rather than dorsiventral, thus the species belongs to *Radiogrammitis*, rather than *Oreogrammitis*. The species is very similar in frond indumentum and dissection to *R. subpinnatifida* (Blume) Parris, but differs in having fewer and much shorter stipes arranged in a series of looser spirals or whorls on the rhizome.

ACKNOWLEDGEMENTS

I wish to thank the Keeper of E for loan of material, the Keeper of K for permission to examine the holdings of Asian and Pacific Grammitids during July 2016, and Ewen Cameron (AK) for expediting the loan from E.

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BOOK REVIEW

- ✓ **FERN NAMES AND THEIR MEANINGS - 2nd EDITION. J.W. Dyce, revised and expanded by J. Edgington. 2016. 59 pp. ISBN O-9509806-1-7. Published by The British Pteridological Society. Price £5.**



The scientific names of plants are often puzzling and their meanings frequently obscure. Many users of these names find their translation and origin fascinating. Finding information regarding the names of ferns and particularly the myriad of cultivar applications is especially difficult. J.W. (Jimmy) Dyce remedied this situation with the publication of this small book in 1988. Proving to be very popular it was reprinted in 1994 but has been difficult to obtain for several years. It is therefore a great pleasure to receive this new edition, greatly expanded and enhanced by Professor John Edgington.

Compared with the first edition, Dyce's original text is mostly retained unaltered, however there are significant additions that considerably improve the utility of the book. Starting with the introduction Dyce gives a brief explanation of history of using Latin for the naming of plants and why it is still used in the modern era. He also alludes to the particular problem of fern cultivar nomenclature, which even today does not seem to be resolved to the satisfaction of all. (The problem arises because many fern cultivar names are actually brief descriptions or polynominals, and were abandoned in other areas of botanical nomenclature centuries ago). The next section, on the etymology of British fern generic names, has been fully revised and expanded by Professor Edgington. It now includes a brief statement regarding the origin of the name as well as the meaning. (Lycophytes were ignored by Dyce in the first edition but are happily now included despite making the book's title slightly imprecise).

The next chapter is completely new, an etymology of non-British genera including all those found in Europe and many that are found in cultivation. I found this part particularly interesting. As in the previous section, both the meaning and origin of the name is given. The next two sections, both helpful and informative, listing the word elements at the beginning and end of fern names, are left unrevised.

The next chapter, again new, comprehensively covers most of the specific names of European ferns including hybrids. This is a most useful addition and many obscure names are included, the exceptions being a large number of *Asplenium* hybrids, many only having been found once.

In 1984 Dyce published an updated list of British ferns and their current names and this has been included here, suitably revised taking into account recent research. Under the same heading, Fern nomenclature – old and new, are two new lists. The first covers non-native species that have recorded growing in the wild in the British Isles and the second is a comprehensive list of synonyms of British ferns and lycophytes. Both these lists are of great interest and will prove to be very useful.

There then follows the largest section of the book, a glossary of fern varietal names. This formed the major part of the first edition and is included here unchanged. Many of the terms are also widely used in species names so it is not restricted to horticultural varieties. Finally there is a new, brief glossary of technical terms and an updated list of references.

As I hope will be appreciated from this review this is a much improved publication where John Edgington has managed to retain the content and spirit of Jimmy Dyce's original but also sought to include much additional relevant and interesting information. He has achieved this most successfully and with the book priced at just £5 it must rank as one of the bargains of the year.

T. Pyner

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STEVENSON, D.W. & LOCONTE, H. 1996. Ordinal and familial relationships of pteridophyte genera. In: CAMUS, J.M., GIBBY, M. & JOHNS, R.J. (Eds) Pteridology in perspective, pp. 435-467. Royal Botanic Gardens, Kew.

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